

Territorial marking in the Yellow mongoose *Cynictis penicillata*: sexual advertisement for subordinates?

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Abstract

In the yellow mongoose, a colonial territorial viverrid, territory marking is performed by all group members. Subordinate adults, both male and female, have higher marking rates than the dominants and juveniles of both sexes and their marks carrying identity cues are deposited especially in border areas and outside the territory. They are also the animals most involved in territorial defence. Within the territory, marking was concentrated around the burrow systems and dominants either did not mark (dominant male) or did not visit (dominant female) the territory borders. Subordinate males, which have low reproductive success in their natal colonies, disperse usually to neighbouring colonies and subordinate females cross territory borders when in oestrus and are mated by males from neighbouring groups. The classes of animal most likely to seek mating opportunities outside the colony thus mark most often where their marks will be encountered by strangers. Apart from its role in territory familiarisation and territory owner assessment, marking in this species is hypothesised as being a means of sexual advertisement for subordinate animals.

Introduction

Marking behaviour has long been regarded as an important component of animal social communication (THIESSEN and RICE 1976), although its function is still obscure. A number of hypotheses to explain why animals mark have been put forward ranging from deterrence of intruders (HEDIGER 1949) to establishment of a familiar smell within the territory (JOHNSON 1973), the latter attempting to explain why animals often mark as frequently inside their territories as on the borders. A more recent hypothesis proposes that scent advertises the identity of a territory inhabitant to an intruder, enabling the latter to assess the holder's status (GOSLING 1982), thus avoiding costly fights. Marking is also considered to be associated with dominance in many species (RALLS 1971; STODDART 1976; BROWN and McDONALD 1985; KAPPELER 1980; SOMERS et al. 1990). Marking behaviour and its relation to dominance is investigated here in a group-living viverrid, the yellow mongoose, *Cynictis penicillata*.

Cynictis is a monotypic genus in the family Viverridae, limited to the southern African subregion (SMITHERS 1983). Feeding habits and reproduction have received some attention (MICHAELIS 1972; HERZIG-STRASCHIL 1977; LYNCH 1980), together with the species' implied role as a rabies vector (ZUMPT 1969, 1976) but little is known of its behaviour (EARLE 1977, 1981). *Cynictis* exhibits a degree of sociality intermediate between the highly social and solitary mongooses (WENHOLD 1990). Group sizes varying from single or paired animals to 10 or more have been reported (ROWE-ROWE 1978; ZUMPT 1976; PRINGLE 1977; DU TOIT 1980; STUART 1981; EARLE 1981; SMITHERS 1983). Animals inhabit a communal burrow system but forage alone. Colonies are territorial, male intruders being chased away while females are tolerated, especially during the mating season (WENHOLD 1990). Defenders are in most cases male residents. Territories are marked by all group members

and this study investigates the various marking modes employed from temporal, spatial and individual aspects.

Material and methods

The study was conducted on Big Island in the Vaal Dam (26° 52" S, 28° 11" E), Transvaal, a temporary island of approximately 200 ha which is a peninsula for most of the year. At least 11 mongoose colonies were present on the island. The study colony consisted of 13 individuals (4 adult ♂♂, 3 adult ♀♀, 5 juvenile ♂♂, 1 juvenile ♀) and was habituated to observer presence during an initial period of 5 months. Adults were animals over 1 year old, juveniles 1 year old or less. The data on which the following analyses were based were collected on a daily basis during the 9 month period subsequent to habituation (April–December 1987) for a total of over 900 h. Mongooses were identified individually by means of natural markings and scars.

Observations were made using 10 × 50 Bencon binoculars. Since marking activities were of short duration, absolute frequency of occurrence of various marking modes were recorded using all events sampling when the animals were in groups and focal animal sampling during foraging (ALTMANN 1973). Observations were timed to cover the entire day from first emergence from the burrow system in the morning to return to the burrow at midday or night. Focal animals were followed for as long a period as possible until they were lost to sight. Focal observations on individuals of less than 15 min duration were not included in the analysis since they would tend to bias the results in favour of areas around the burrow systems. A different focal animal was selected each day to prevent continuity effects. Data were entered into a computer using a standard database program and further analyses were conducted using standard statistical packages. Statistical tests used are mentioned at appropriate points in the text and the level of probability given is two-tailed in all cases.

Marking frequency

Since the time periods over which individuals were observed varied, and different focal animals were observed on different days, rates of marking were calculated (mean rate/h/day/animal) to allow comparison between individuals. For statistical analyses, the daily rates of occurrence were considered independent since observations on the same animal were separated by at least seven days. Individual marking rates were calculated separately for the five different modes of marking observed.

Location of marking sites

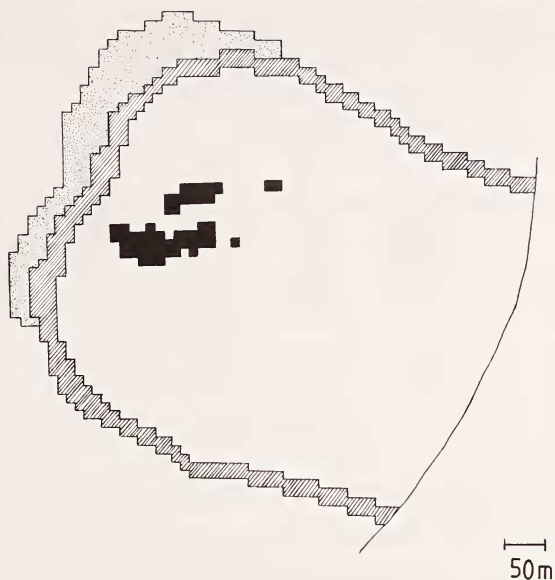
The 21,300 m² territory was divided into 10 × 10 m grid squares to determine marking frequency in various areas. The rate of occurrence of marking in each grid square was then calculated i.e. mean marking frequency/h that the animal was observed in a particular square. Grid squares were then allocated to four categories: a. inside the territory but not in the vicinity of a burrow, b. within the territory and containing a burrow, c. on the territory border, d. outside the territory (Figure). The territory border was considered as the approximately 20 m wide fringing strip which was as far as an animal would either chase an intruder out of its territory or, conversely, how far it was chased after intruding in the neighbouring territory. The rates of occurrence of various marking behaviour patterns were determined for the four areas. The marking rates of various classes of animal in the same area were also calculated.

Results

Description of marking activities

Cynictis marks objects by four means. Anal marking, using secretions of the peanut-sized anal glands on either side of the anus, is the most common. The animal squats with the tail arched and presses the glands briefly on the substrate. Sniffing the site usually precedes marking and may follow it. In general, only a single mark is deposited on a low object, usually a stone or branch. A handstand posture typical of several other viverrids was not observed and anal dragging was rare.

Objects are also marked with a glandular area on the cheek using a wiping motion, sometimes repeated with the same or the alternate cheek. The object is stroked in a continuous movement from snout to eye. Typical objects are branches and patches of bare earth, small objects being steadied with the forepaws. The action is often preceded by



The territory of the study colony divided into $10 \times 10 \text{ m}^2$ grid squares. The shoreline of the island is on the right. Shaded squares contain burrows, open squares are territory areas without burrows, hatched squares indicate the border of the territory and dotted squares show the areas outside the territory that were visited by group members

sniffing, and frequently followed by wiping the entire side of the body on the ground, termed side-wiping. The functional significance of the latter is not clear, since there does not appear to be any epidermal glandular tissue in this region of the body. However, side-wiping sites are often covered with dried mongoose faeces and it is possible that this behaviour is a form of "self-anointing", faecal odour being transferred by this means from one site to another. Frequently used side-wiping sites, which are usually situated next to a bush or a clump of grass, are recognisable as depressions in the ground devoid of any debris except the faeces deposited there at intervals.

Defaecation and urination can be considered as secondary ways of marking a territory. Specific defaecation sites (middens) are present, at least one being situated near every set of burrows. On emerging from the burrows in the morning, one of the first actions is to approach the midden, sniff at the faeces present, and then defaecate. This is performed from a squat with the tail arched as in anal marking, but without the anus touching the ground. Animals also defaecate at communal sites scattered throughout the territory and usually associated with secondary burrows. These are burrows used, usually by single animals, to sleep in during the heat of the day or occasionally overnight. The faeces, especially, have a strong and distinct odour, possibly from secretions of the anal gland covering them.

The same squatting posture is used by both sexes during urination, which also takes place primarily at middens, although dominant females may also urinate with one hind leg lifted. Urination also occurs at sites throughout the territory during foraging excursions.

Marking frequency

The daily rates/h of various marking modes were calculated for each animal and their means determined. The mean rates for different sex and age classes are shown in table 1.

Table 1. Mean marking rates per hour for different sex and age classes

Class	N	Mean marking rate/hour					
		am	sw	cw	sm	ur	def
Dominant male	1	0.54	0.02	0.20	0.75	0.0	0.39
Subordinate adult males	3	0.83	0.46	0.55	1.83	0.06	0.47
Juvenile males	5	0.41	0.32	0.31	1.04	0.14	0.61
All adult males	4	0.75	0.37	0.46	1.58	0.04	0.45
All males	9	0.56	0.34	0.37	1.27	0.10	0.54
Dominant female	1	0.11	0.07	0.10	0.28	0.0	0.68
Subordinate adult females	2	0.20	0.28	0.15	0.63	0.11	0.38
Juvenile females	1	0.0	0.0	0.0	0.0	0.0	0.56
All adult females	4	0.16	0.20	0.13	0.49	0.07	0.50
All females	5	0.15	0.18	0.12	0.44	0.06	0.50
All Adults	7	0.47	0.29	0.30	1.06	0.05	0.47
All Juveniles	6	0.38	0.29	0.29	1.00	0.13	0.61

am = anal marking, sw = side wiping, cw = cheek wiping, sm = scent marking (sum of am + sw + cw), ur = urination, def = defaecation.

Anal marking (am), cheek wiping (cw) and side-wiping (sw) rates were added to give a mean scent marking (sm) rate. The data following were tested for significant differences using the Mann-Whitney U-test.

Subordinate adult males have a significantly higher anal marking rate than the dominant male ($p < 0.05$). Males in general anal mark significantly more than females, whether only adults ($p < 0.05$) or all age groups of both sexes are compared ($p < 0.01$). Subordinate adult males also side-wiped significantly more than the dominant ($p < 0.05$) and adult males more than adult females ($p < 0.05$). All males side-wiped significantly more often than all females ($p < 0.02$). For cheek wiping, the only significant difference found was for subordinate males, which have a higher rate than the dominant ($p < 0.05$). Although not significant, all males tend to cheek wipe more than all females ($p < 0.07$).

Subordinate males also had a higher rate of scent marking in general than the dominant male ($p < 0.0005$) and subordinate females marked more than the dominant female ($p < 0.05$). Adult males had a higher marking rate than adult females ($p < 0.02$) and juvenile males a higher one than the juvenile female ($p < 0.02$). All males together thus scent mark more than all females ($p < 0.002$).

No significant differences were found between any of the age and sex classes for urination and defaecation ($p > 0.05$) but subordinate adult males had significantly higher defaecation rates than the dominant male ($p < 0.05$).

Location of marking sites

The rate of occurrence per hour of various types of marking was determined for each individual in each grid square in which it was observed. The mean data for age and sex classes in each of the four areas are shown in tables 2–5.

In grid squares containing a burrow system (Tab. 2), the only significant difference found was between adult and juvenile males, adult males having a significantly higher rate of scent marking in general than juveniles ($p < 0.001$; $p > 0.1$ in all other cases).

No significant differences were found in marking rates between any age or sex category in grid squares within the territory which did not contain a burrow system (Tab. 3), ($p > 0.1$ in all cases).

Adult males anal marked and side-wiped in the border area significantly more than

juvenile males ($p < 0.05$, Tab. 4). Their rate of all scent marking activities combined was also significantly higher than that of juveniles ($p < 0.01$). The dominant male was never observed marking on the border although he visited it. The dominant and the juvenile females were also never seen on the border of the territory throughout the study period. The data for females is therefore based only on observations from subordinate adults. Subordinate adult females anal marked the border area significantly more than juvenile

Table 2. Mean marking rates in territory grid squares containing a burrow system

Class	N	Mean marking rate/hour					
		am	sw	cw	sm	ur	def
Dominant male	1	0.24	0.0	0.24	0.48	0.0	0.0
Subordinate adult males	3	0.54	0.29	0.24	1.07	0.06	0.06
Juvenile males	5	0.42	0.33	0.24	0.98	0.04	0.07
Dominant female	1	0.10	0.02	0.05	0.17	0.09	0.03
Subordinate adult females	2	0.18	0.02	0.09	0.29	0.01	0.10
Juvenile females	1	0.0	0.0	0.0	0.0	0.0	0.0

am = anal marking, sw = side wiping, cw = cheek wiping, sm = scent marking (sum of am + sw + cw), ur = urination, def = defaecation.

Table 3. Mean marking rates in territory grid squares without a burrow system

Class	N	Mean marking rate/hour					
		am	sw	cw	sm	ur	def
Dominant male	1	2.50	0.0	0.0	2.50	0.0	0.0
Subordinate adult males	3	0.23	0.70	0.24	1.17	0.02	0.04
Juvenile males	5	0.48	1.01	0.25	1.74	0.02	0.05
Dominant female	1	0.0	0.0	0.0	0.0	0.0	0.0
Subordinate adult females	2	0.11	0.08	0.05	0.23	0.0	0.01
Juvenile females	1	0.0	0.0	0.0	0.0	0.0	0.0

am = anal marking, sw = side wiping, cw = cheek wiping, sm = scent marking (sum of am + sw + cw), ur = urination, def = defaecation.

Table 4. Mean marking rates for grid squares on the territory border

Class	N	Mean marking rate/hour					
		am	sw	cw	sm	ur	def
Dominant male	1	0.0	0.0	0.0	0.0	0.0	0.0
Subordinate adult males	3	4.67	4.91	2.08	11.66	0.05	0.36
Juvenile males	5	1.49	2.75	0.78	5.02	0.57	0.26
Dominant female	1	0.0	0.0	0.0	0.0	0.0	0.0
Subordinate adult females	2	2.40	0.0	1.11	3.51	0.0	0.21
Juvenile females	1	0.0	0.0	0.0	0.0	0.0	0.0

am = anal marking, sw = side wiping, cw = cheek wiping, sm = scent marking (sum of am + sw + cw), ur = urination, def = defaecation.

($p < 0.05$) but not subordinate adult males and were never observed side-wiping or urinating there.

Subordinate adult males had a significantly higher rate of scent marking in outside the territory than did juvenile males ($p < 0.001$, Tab. 5). Amongst females, only the juvenile had a significantly higher rate of defaecation outside the territory than the subordinate adults ($p < 0.001$). Females were never observed side-wiping outside the territory.

Table 5. Mean marking rates for grid squares outside the territory

Class	N	Mean marking rate/hour					
		am	sw	cw	sm	ur	def
Dominant male	1	0.31	0.0	0.0	0.31	0.0	0.0
Subordinate adult males	3	4.39	3.05	1.10	8.54	0.14	0.01
Juvenile males	5	1.44	0.55	0.02	2.01	0.0	0.23
Dominant female	1	0.0	0.0	0.0	0.0	0.0	0.0
Subordinate adult females	2	0.04	0.0	0.16	0.20	0.04	0.04
Juvenile females	1	0.0	0.0	0.0	0.0	0.0	1.15

am = anal marking, sw = side wiping, cw = cheek wiping, sm = scent marking (sum of am + sw + cw), ur = urination, def = defaecation.

Comparison between areas

To determine whether different classes of animals showed significant differences in marking modes in various areas of the territory, rates were compared using the Kruskal-Wallis test (SIEGEL 1956). The level of significance in all cases is 0.05. Since this test compares the mean of the ranks given to the data points in the samples, the results in some cases do not appear to reflect the differences between the mean rates shown in the tables.

For grid squares containing a burrow system vs those in the remainder of the territory, the following significant differences were found: adults anal marked and cheek wiped significantly more often in the vicinity of the burrows than elsewhere in the territory, juveniles showing the opposite tendency. There were no differences between side-wiping rates, except for juvenile males which performed this behaviour significantly less often near burrows. For all classes of animals, defaecation and urination take place more often near burrows than in the remainder of the territory.

Anal marking, side-wiping and cheek wiping rates were all higher on the border than in areas of the territory away from the burrow systems for all classes of animal. Males defaecated more on the border than did females. Only juvenile males urinated more on the border than inside the territory away from the burrows. All other differences were non-significant.

A comparison of border areas with areas around burrow systems showed a significantly higher rate of anal marking at the border for subordinate males and females while the opposite was true of juvenile males and the two dominant animals. Subordinate adult males also had a higher rate of side-wiping at border vs burrow areas than females. Juvenile males showed no significant difference. The reverse was true for cheek wiping. Here, juvenile males cheek wiped more at the border than near burrows, other classes of animal showing no difference. No differences were found for defaecation in the two areas. Subordinate adult males, however, had higher urination rates near burrows.

Comparison of marking rates between grid squares on the border and those outside the territory in which group members were observed showed that subordinate adult males and females had a higher rate of anal marking on the border than outside it. Other classes of

animals, with the exception of the dominant female who did not visit the border, anal marked equally frequently in both areas. No female side-wiped outside the territory, otherwise all classes had significantly higher side-wiping and cheek wiping rates on the border than outside. Defaecation was significantly higher outside the territory for subordinate adult males while subordinate adult females and juvenile males showed no significant difference. Juvenile males, however, urinated more outside the territory than on the border.

Marking and territorial defence

The frequency with which individuals marked/10 h and were observed attacking and chasing intruders in the territory/10 h shown in table 6. There was a highly significant relationship between marking and territorial defence (Spearman's rho correlation, $r_s = 0.7701$, $N = 12$, $p = 0.03$). Of all ♀♀ only subordinate ♀2 was observed to attack strangers, the majority of the defence activities being performed by the adult and older juvenile males.

Table 6. Mean rates/10 hours of attacking intruders and marking for each group member

	Adult ♂♂			Adult ♀♀			Juv. ♂♂				Juv. ♀	
	1	2	3	1	2	3	1	2	3	4	5	1
Attacks												
	2.1	2.4	1.1	0	1.0	0	0.4	1.0	0.7	0	0	0
Marking												
	7.5	25.3	18.3	2.8	2.5	6.2	4.6	16.8	15.9	1.6	1.9	0.2

Discussion

Probably the most interesting aspect of this study is that all modes of territorial marking are performed more frequently by subordinate adults than by dominant ones, in contrast to EARLE's (1977) statement. This is not typical for mammals (see RALLS 1971; EISENBERG and KLEIMAN 1972 and BROWN and MACDONALD 1985 for reviews) where dominant males, especially, are the ones most involved in territorial advertisement and defence. However, in the yellow mongoose, it is the subordinate adult males which are more involved in territorial defence than the dominant male and have their highest marking rates at the territory border and in fringing areas.

The finding that males mark more in general than females has its parallels in other mammalian species (JOHNSON 1973; THIESSEN and RICE 1976). Although a tendency for adults to mark more than juveniles has been reported in the literature (THIESSEN and RICE 1976), this was not substantiated for the yellow mongoose. Adult males marked more than juvenile males, but this was not true for adult females. There was a strong correlation between marking and active territorial defence in this species, females playing little part in the latter. The study period coincided with puberty onset in the juveniles and for a related species, the dwarf mongoose *Helogale undulata*, juveniles were found to be amongst the most active group members in territorial defence (RASA 1977) and also to have high marking rates (RASA 1973). Thus the finding that juvenile males mark as often as adults may reflect their active role in territory protection.

The study has also shown that the areas most frequently marked by subordinate males and females are sites at the territory border and in fringing areas while the dominant female and juvenile females never visit the border, confining their marking to the territory interior around the burrows. The dominant male also marks predominantly within the territory.

Adult subordinate males anal mark and sidewipe most frequently at the border and outside the territory, subordinate adult females anal mark most frequently there. These marking modes are the ones most likely to carry identity cues, as has been found in both dwarf mongooses (RASA 1973) and small Indian mongooses *Herpestes auro punctatus* (GORMAN 1976). Juveniles urinate and cheek wipe most frequently in border areas, juvenile males extending the increased urination rate to sites fringing the territory. Cheek wiping and urination carried no identity cues in dwarf mongooses (RASA 1973) but cheek wiping was indicative of high excitement. Juvenile marking in border areas is thus likely to have other connotations than that of the subordinate adults.

The data suggests that both JOHNSON'S (1973) familiarity hypothesis and GOSLING'S (1982) assessment hypothesis may apply to the yellow mongoose. The high marking rates observed in territory areas containing a burrow system as opposed to those without one suggest that odour is preferentially deposited near major resting sites. The concentration of marks around burrows is more likely to be associated with provision of a familiar odour for inhabitants rather than with intruder deterrence, concurring with JOHNSON'S hypothesis. GOSLING'S hypothesis, however, suggests that marks within a territory should be evenly distributed to increase an intruder's likelihood of encountering them and enabling it to assess the territory owner. The tendency to mark outside the territory using modalities carrying identity cues, with the highest scent marking rate occurring on the border, may establish an odour gradient external to the territory itself, indicating to an intruder the perimeter within which it can expect attack. Since yellow mongooses from different groups frequently encounter each other outside their territory borders, assessment may take place before the territory is penetrated. These marks have no deterrent effect, intruders sniffing them and then continuing on into the territory, as found for other carnivores (LEYHAUSEN 1965; SCOTT 1967), HEDIGER'S (1949) deterrence hypothesis does not appear to hold for this species.

The surprising finding that it is the subordinate adult males and subordinate females that mark more at the border than within the territory, and that the dominant animals rarely visit these areas, suggests that these marks may serve a second advertising purpose for subordinates. Subordinate males disperse from their natal group when adult, usually to neighbouring groups (WENHOLD 1990), as do subordinate females. Females also cross territory borders when in oestrus and are mated by males from a neighbouring group (WENHOLD 1990). The deposition of anal gland scent in areas where it is most likely to be encountered by neighbours may serve to advertise the age, sex and reproductive state of the marker, as well as familiarising members of neighbouring groups with the marks of potential immigrants and possibly facilitating the transfer of individuals between colonies.

Animals unlikely to disperse or mate or be mated outside the colony either never visited the territory border (the dominant and juvenile females), did not mark there (the dominant male), or had low rates of identity carrying marks in this area (juvenile males). Since the marking frequency of subordinate females does not appear to correlate with territorial defence activities as it does in males, another hypothesis to explain this high female marking rate on the border is suggested. By depositing the majority of their identity carrying marks in border areas, subordinate females may utilise odour cues to advertise their presence to neighbouring males for future mating purposes. For subordinate males, which are likely to have no reproductive success with females in their natal colonies (WENHOLD 1990; RASA et al. 1992), high marking rates on the border may also be a means of advertising their existence to neighbouring females, with which they have been observed to mate. Marking in this species may thus not only play a role in assessment for intruders and familiarity for territory inhabitants but may also serve a secondary purpose as a major means of sexual advertisement for subordinates, especially females, to attract prospective mates from neighbouring territories.

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Zusammenfassung

Territoriumsmarkierung bei der Fuchsmanguste Cynictis penicillata: sexuelle „Reklame“ für untergeordnete Tiere?

Bei der Fuchsmanguste (*Cynictis penicillata*), einer in Kolonien lebenden Viverridenart, wird Territoriumsmarkierung von allen Gruppenmitgliedern durchgeführt. Adulte untergeordnete Tiere, sowohl Männchen als auch Weibchen, markieren häufiger als dominante und juvenile Tiere beiderlei Geschlechts. Die Duftstoffe, die Identitätsmerkmale beinhalten, werden besonders an Territoriumsgrenzen und außerhalb des Territoriums abgelegt. Adulte subordinate Gruppenmitglieder sind zudem in der Verteidigung des Territoriums am aktivsten. Innerhalb des Territoriums findet Markierung hauptsächlich um die Wohngänge herum statt, und dominante Tiere markieren entweder nicht an den Territoriumsgrenzen (dominantes Männchen) oder besuchen das Grenzgebiet nicht (dominantes Weibchen). Untergeordnete Männchen, die einen geringeren Fortpflanzungserfolg innerhalb der Gruppe aufweisen, wandern gewöhnlich in benachbarte Territorien ab. Untergeordnete Weibchen überqueren die Territoriumsgrenze, wenn sie im Oestrus sind, und werden auch von Männchen der benachbarten Gruppen begattet. Folglich markieren gerade die Tiere, die am ehesten Fortpflanzungsmöglichkeiten außerhalb der Geburtskolonie suchen, häufiger in einem Gebiet, wo der Duft von Koloniefremden angetroffen werden kann. Es wird die Hypothese aufgestellt, daß Markieren bei dieser Art außer als Vertrauenszeichen und Besitzanspruch des Territoriuminhabers darüber hinaus als Mittel zur sexuellen „Reklame“ für untergeordnete Tiere eingesetzt wird.

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